



A river runs through it: Land-use and the composition of vegetation along a riparian corridor in the Cape Floristic Region, South Africa

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ABSTRACT

Riparian zones are important for the many ecosystem services they supply. In settled areas, the vegetation of such zones is shaped by human land-use; this often creates conditions under which alien plant species thrive. Alien plants have been shown to induce large-scale changes in riparian habitats, and they pose a major threat to the continued provision of key ecosystem services. We used direct gradient analysis to assess correlations between land-use and the composition of vegetation along a riparian river corridor in the highly transformed landscape surrounding Stellenbosch in South Africa's Western Cape Province. Vegetation plots were sampled along the entire length of the river from headwaters to estuary (ca. 40 km). Plant community composition was analyzed in relation to land-use data collected in the field, and additional land-use variables computed from digital land-cover data. Patterns of plant community structure were found to be directly related to land-use, with measures of cover, richness, and diversity differing significantly among land-use types. Portions of the riparian zone adjacent to agricultural land had the greatest level of alien plant cover, while areas bordered by urban land maintained the highest alien species richness. Areas adjacent to grazing and natural lands showed intermediate and low levels of invasion, respectively. Several native species were found to persist in areas with high abundance and diversity of invasive alien plants, suggesting that they will be valuable focal species for future restoration attempts. Due to the level of human-mediated change in many areas of the riparian zone, restoration to historic conditions over most of the river is not considered feasible. These areas should be recognized as examples of novel ecosystems, and management efforts should focus on restoring or creating desirable ecosystem functions, rather than on achieving assemblages comprising only native species.

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1. Introduction

In many human-transformed landscapes, riparian zones represent the last remaining areas of semi-natural habitat. These zones provide important ecosystem services, including riverbank stabilization, nutrient cycling, flood attenuation, regulation of stream flows and stream temperatures, groundwater recharge, and water purification (Kauffman et al., 1997; Tickner et al., 2001). Riparian habitats also provide refuge for wildlife in urban and rural areas and act as corridors for movement of species and transport of plant propagules (Forman and Godron, 1986; Naiman and Decamps,

1997; Botkin and Beveridge, 1997). In many areas, riverine corridors play a key role in planning for conservation in the face of global climate change, both to safeguard routes for migration and to allow for exchange between inland and coastal biotas (Rouget et al., 2003). Riparian areas increase the aesthetic value of agricultural and urban landscapes and expand opportunities for outdoor activity (Postel and Carpenter, 1997). These services are of particular value in developing areas of the world, where many people rely upon rivers for irrigation, drinking water, and recreation.

With the possible exception of recreation, all of these ecosystem services are ultimately governed by the composition of vegetation along riparian zones (Naiman and Decamps, 1997; Sweeney et al., 2004). As riparian zones are the focus of concentrated human activity, this vegetation is very often shaped by human-mediated disturbances (Holmes et al., 2005). Intensive land-use along riparian areas may lead to increased soil erosion and sedimentation in rivers, increased nutrient inputs, and increased availability of physical resources such as light (Davis et al., 2000; Holmes et al.,

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2008). Coupled with reduced flooding as a result of water impoundment or abstraction, human-usage factors may be responsible for creating ideal conditions for the establishment, proliferation and spread of alien plants (Richardson et al., 2007). Such species often attain high densities, and are frequently associated with degradation of riparian habitats (Richardson et al., 2007; Holmes et al., 2008). Among the many changes associated with invasion of alien plants in riparian areas are: alteration of river channel morphology (Rowntree, 1991), reduced recruitment of native species as a result of changes in canopy cover (Galatowitsch and Richardson, 2005), and increased transpiration leading to reduction in flows (Dye and Jarman, 2004). Alien plants can further reduce key ecosystem services provided by riparian zones by affecting flood patterns, water table levels, and soil moisture conditions (Tickner et al., 2001). Concurrently, anthropogenic activity in the surrounding landscape may facilitate growth of alien plant populations by modifying environmental conditions and establishing new sources of propagules (Hobbs, 2000; Foxcroft et al., 2007, 2008). Despite these connections, few attempts have been made to assess the effects of land-use on patterns of alien invasion in riparian zones.

It is important to understand how anthropogenic activities affect riparian areas so that informed decisions can be made regarding management, conservation and restoration of these habitats. As so few studies have addressed the impact of surrounding land-use on the structure of riparian ecosystems, there is very little scientific foundation on which to base objective recommendations for mitigation. Human-mediated changes have often led to a complex gradient of land uses adjoining riparian ecosystems. In order to study how this gradient of land uses affects patterns of biodiversity, it is useful to employ the process of direct gradient analysis (Whittaker, 1967). Direct gradient analysis addresses the composition and function of ecosystems in relation to a set of external environmental variables. Performing direct gradient analysis in a landscape characterized by anthropogenic disturbance allows an examination of the role of land-use in explaining ecological patterns (McDonnell and Pickett, 1990). Knowledge garnered from such studies can then be utilized for the institution of effective riparian corridor management.

This study aims to examine changes in riparian plant community composition along a gradient of land-use types (natural, urban, agricultural, and communal grazing) for the Eerste River corridor located in the Cape Floristic Region of South Africa. Specific goals of the study are to: (1) assess whether riparian plant composition is influenced by adjacent and surrounding land uses; (2) determine whether patterns of alien plant composition can be explained by these human-usage characteristics; and (3) to identify species of native riparian plants that persist in areas of high alien invasion.

As with any study of land-use along river systems, specific correlations between vegetation structure and land-use will always vary in riparian zones across different landscapes. The Eerste River has a particular spatial configuration of land-use, and the patterns of plant community structure found along the Eerste River may not occur in riparian areas with different land-use sequences. Nevertheless, the Eerste River provides a classical example of river systems in mediterranean-climate regions which often have relatively pristine upper catchments, but have been heavily transformed by anthropogenic activities in the lower reaches of the river. As such, the concepts and patterns presented here should be of interest to managers of riparian areas in other mediterranean-climate zones. Furthermore, we know of no other study that has explored these issues in detail along the entire length of a river; this study will therefore be useful as a baseline for further research and comparison.

2. Methods

2.1. Study area

The source of the Eerste River lies in the Jonkershoek Mountains at an altitude of 530 m, approximately 60 km east of Cape Town in the Western Cape Province of South Africa. From Jonkershoek, the river flows in a north-westerly direction into the town of Stellenbosch, where it turns south and ultimately discharges into the Atlantic Ocean in False Bay at Macassar (Fig. 1). The Eerste River is approximately 40 km long, with a catchment area of 420 km². Along its route to Macassar, the river receives flows from several major tributaries, with bank-to-bank width increasing from an average of 5 m near the headwaters to an average of 14 m in the lower river zone. The average gradient of the river ranges from 24 m/km in the mountain stream zone to an average of 2 m/km in the lower reaches of the river (King, 1981). The Eerste River catchment lies in a mediterranean-climate zone with hot, dry summers and cool, wet winters. At 4000 mm per annum, the upper reaches of the river receive some of the highest recorded rainfalls in South Africa, while the lower reaches receive as little as 570 mm per annum (DWAF, 2004).

The landscape surrounding the Eerste River supports a number of land uses including various forms of agriculture (vineyards, orchards, and crop production), commercial forestry, and communal grazing, as well as domestic use in highly urbanized residential areas. Stellenbosch (human population ca. 117,000) is the main urban area along the river, with additional urban development present in Macassar. Currently, forestry plantations of *Pinus radiata* exist in the landscape surrounding the upper reach of the river, although a wide buffer zone of natural fynbos vegetation has been maintained between the river and plantation areas. Approximately the first 6 km of the upper river is bordered by natural vegetation and relatively unaffected by human influence. Since 1981, the upper reach of the river has been regulated by the Kleinplaas Dam, above which the Eerste River is perennial (DWAF, 2004). The Kleinplaas Dam overflows during winter, and compensation releases are made from the dam during summer to provide water for downstream users. The river is canalized in places as it flows through the town of Stellenbosch, after which it is joined by the Plankenburg River. At this confluence, water is abstracted by the local Irrigation Board, which has an additional abstraction point just above the confluence with the Blouklip River. The river is subject to further abstraction by owners of riparian properties for most of its length. Treated municipal effluent from the Stellenbosch Waste Water Treatment Works enters the river through the Veldwagters tributary. Below the confluence of the Veldwagters and Eerste Rivers, this treated effluent is a major component of river flow during the summer months (DWAF, 1993).

2.2. Field sampling

A detailed survey of the vegetation of the riparian zone was undertaken along the entire length of the Eerste River from headwaters to near the estuary. Field data were collected between mid-September and mid-December 2008 (i.e. spring), during which time most herbaceous species should be apparent. Plots were paired at intervals of 500 m along both banks of the river, for a total of 150 plots. In order to capture all species of regular occurrence, plot sizes were adjusted depending upon structure of the vegetation community at each plot location. Herb-dominated communities were sampled with plot areas of 20 m², shrublands/thicket with an area of 50 m², and forest communities with an area of 100 m². Plots were primarily rectangular in shape, with the longest edge placed perpendicular to the river. Decisions regarding plot

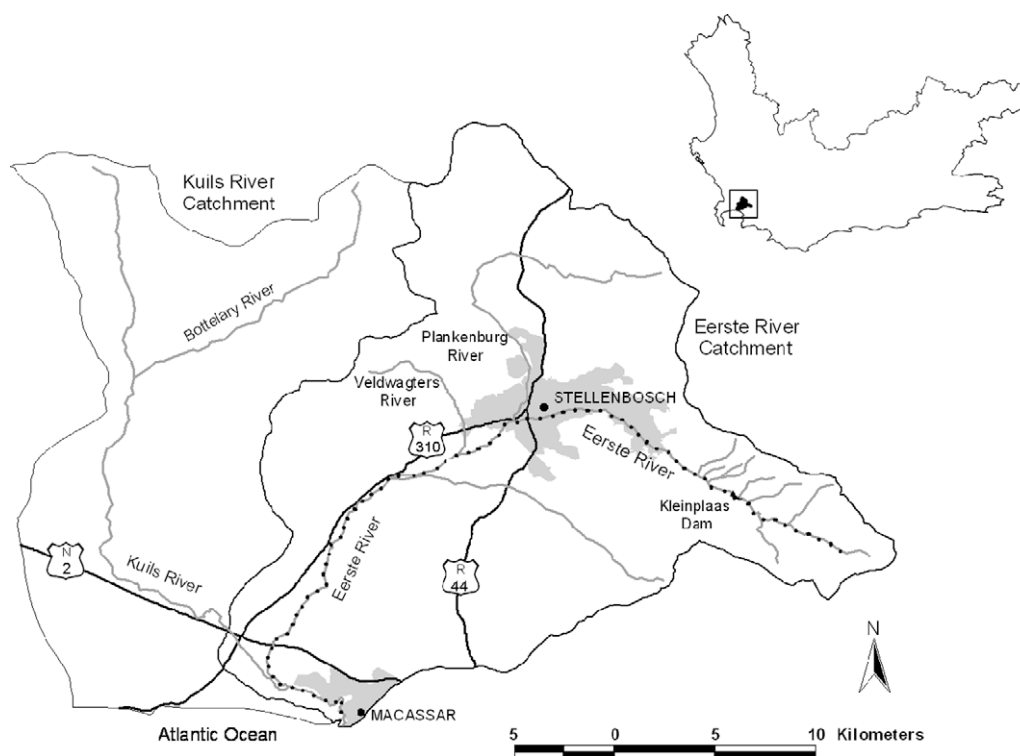


Fig. 1. Map of the study area showing its location in the Western Cape, South Africa. Sampling points along the river are indicated by (●). Shaded areas indicate areas of urban development.

size were adapted from values suggested in Westhoff and van der Maarel (1973).

Plot edges were extended to bankfull margins and locations were recorded using a Garmin GPS Map76 handheld Global Positioning System (GPS). Multiple photographs were taken of each plot (images are archived at the Centre for Invasion Biology, Stellenbosch University). Several environmental features were described at each site including inclination, aspect, geomorphology, and substrate. Adjacent land-use and any evidence of disturbance were also noted. All plant species within each plot were recorded, and an estimation of height and absolute cover for each species was made. Species were labeled as native or alien following the criteria of Pyšek et al. (2004) and using published floras including Goldblatt and Manning (2000), Henderson (2001) and Bromilow (2005). Species which could not be positively identified in the field were collected and labeled with a unique specimen number. Identifications were made at the Bolus Herbarium (BOL), University of Cape Town, with determinations verified by the curator, Dr. Terry Trinder-Smith. The collections have been archived in the Centre for Invasion Biology at Stellenbosch University.

Surface soil samples were collected at each plot and analyzed for pH (KCl solution), total carbon content, and electrical resistance. Soil cation concentrations of sodium, calcium, magnesium, potassium, and phosphorous were also measured.

2.3. Landscape characterization

Digital topographical data were used to determine the longitudinal position of each plot along the length of the river (measured as distance from headwaters) and the approximate elevations of each plot (in conjunction with field GPS estimates). ArcView (version 3.3, Environmental System Research Institute, 2002) was used to analyze digital land-cover data supplied by the South African Department of Water Affairs and Forestry (DWAF). Accuracy of

land-cover classification surrounding the river was verified by visually comparing land-cover data to high-resolution color aerial photos taken in February 2005, March 2005, and June 2007. Eight environmental variables were calculated from the land-cover data to serve as components of land-use along the river and are listed in Table 1.

2.4. Data analysis

Total absolute cover and species richness of both native and alien species were calculated for each plot, each land-use type, and for the river as a whole. Distribution ranges were determined for common alien plants in order to examine patterns of invasion for individual plant species. These were then assessed in relation to adjacent land-use to determine whether individual species ranges could be associated with particular land-use types.

Table 1
Description of codes for environmental variables used in analysis of data.

Variable code	Description
D-Road	Distance from plot to the nearest paved road (km)
D-Rail	Distance from plot to the nearest railroad (km)
R-Dens	Density of roads within a 500 m radius of plot (km)
A-Area	Hectares of agricultural land within a 500 m radius of plot
G-Area	Hectares of communal grazing land within a 500 m radius of plot
N-Area	Hectares of natural (untransformed) land within a 500 m radius of plot
P-Area	Hectares of forestry plantation within a 500 m radius of plot
U-Area	Hectares of urban/suburban development within a 500 m radius of plot
Grazing	Land-use immediately adjacent to plot is communal grazing
Agric	Land-use immediately adjacent to plot is agriculture
Urban	Land-use immediately adjacent to plot is urban/suburban development
Natural	Land immediately adjacent to plot is untransformed

Table 2

Correlation among environmental variables for 150 study plots along the Eerste River riparian corridor. Numbers in the lower portion of the table indicate Pearson's product-moment correlation coefficients, while numbers in the upper portion represent corresponding *P*-values. Variables were considered highly correlated at values ≥ 0.80 or ≤ -0.80 . Asterisks indicate variables used in final analyses. Refer to Table 1 for description of codes.

	D-Road	D-Rail	R-Dens	A-Area ⁺	G-Area ⁺	N-Area ⁺	P-Area	U-Area ⁺	Grazing ⁺	Agric ⁺	Urban ⁺	Natural
D-Road	1	>0.001	>0.001	>0.001	0.017	>0.001	>0.001	>0.001	0.111	0.002	>0.001	>0.001
D-Rail	0.81	1	>0.001	>0.001	0.033	>0.001	>0.001	0.003	0.288	>0.001	0.208	>0.001
R-Dens	−0.467	−0.294	1	>0.001	0.007	0.001	0.029	>0.001	0.045	>0.001	>0.001	0.016
A-Area ⁺	−0.296	−0.532	−0.390	1	>0.001	>0.001	>0.001	>0.001	>0.001	>0.001	0.021	>0.001
G-Area ⁺	−0.194	−0.174	0.219	−0.468	1	0.004	0.093	0.016	>0.001	0.007	0.749	0.009
N-Area ⁺	0.836	0.941	−0.266	−0.526	−0.231	1	>0.001	0.076	0.138	>0.001	0.064	>0.001
P-Area	0.366	0.490	−0.178	−0.289	−0.138	0.397	1	0.073	0.225	>0.001	0.052	>0.001
U-Area ⁺	−0.287	−0.239	0.804	−0.476	0.196	−0.145	−0.147	1	0.027	>0.001	>0.001	0.160
Grazing ⁺	−0.131	−0.087	0.164	−0.346	0.601	−0.122	−0.100	0.181	1	>0.001	0.019	0.025
Agric ⁺	−0.247	−0.553	−0.329	0.784	−0.219	−0.511	−0.256	−0.359	−0.306	1	>0.001	>0.001
Urban ⁺	−0.312	−0.103	0.458	−0.188	0.026	−0.151	−0.159	0.402	−0.191	−0.489	1	>0.001
Natural	0.712	0.833	−0.196	−0.490	−0.213	0.858	0.543	−0.115	−0.184	−0.471	−0.293	1

Simpson's index (*D'*) and Pielou's evenness index (*J*) were used in order to examine the relationship between adjacent land-use and species diversity. Values were calculated for each plot using the vegetation classification and analysis software package JUICE version 7.0 (Tichý, 2002). The relationship between adjacent land-use and these diversity measures, as well as cover and richness of alien and native species, was analyzed using Kruskal–Wallis one-way analysis of variance (ANOVA) in the statistical analysis program SPSS version 15 (SPSS, 2006). Mann–Whitney U tests were subsequently used in order to determine how these effects differ between land uses. Due to a pronounced “dust bunny” distribution (i.e. many zero values) in much of the species data (McCune and Grace, 2002), parametric tests could not be used.

Vegetation and environmental data were further analyzed with canonical correspondence analysis (CCA; Ter Braak, 1986), using the multivariate ecological software package Canoco 4.5 (ter Braak and Šmilauer, 2002). CCA is a method for direct gradient analysis which can be used to detect patterns in species and/or plots which have been constrained by a set of external environmental variables (Legendre and Legendre, 1998). In addition to the eight environmental variables calculated using GIS, land-use data collected in the field were coded as categorical variables and included in the CCA (Table 1). This allowed for examination of land-use effects at two different scales: effects of land-use immediately adjacent to the river as well as the effects of land-use from a broader landscape perspective. Elevation and Distance from headwaters were initially included as environmental variables as well, but analysis showed them to be confounded with several other variables including Distance to nearest road, Distance to nearest railroad, and hectares of natural area. Furthermore, they were found to have variance inflation factors (VIF) greater than 50 (hence being highly redundant due to covariance patterns; Ter Braak, 1986) and were thus removed from the analyses. Exclusion of these two variables led to stabilization of the other VIFs. Multicollinearity was examined among the remaining environmental variables in order to determine whether there were other variables that should be dropped from analysis. Variables such as Distance to road, Distance to rail, and Adjacent natural land were all found to be highly correlated with hectares of natural area ($r = 0.83$; 0.94 ; 0.87), and were thus removed from further analysis. Road density was also removed due to high correlation with hectares of urban area ($r = 0.80$). Hectares of forestry plantation was removed when post hoc analyses found that it explained very little variation beyond what was already explained by hectares of natural area. The remaining variables were not highly inter-correlated (Table 2.) and were used as independent variables in the CCA. Statistical significance of the relationship between species composition and the environmental variables was determined using a Monte Carlo test with 1000 permutations.

3. Results

A total of 246 plant species were identified along the river, of which 131 were alien and 115 were native (Appendix A). Of the alien species, 21 are listed as Category 1 invaders in South Africa (Government Gazette, 2001), and 12 have been proposed as emerging invaders per Nel et al. (2004). Alien species accounted for 62% of the overall vegetation cover along the Eerste River riparian corridor. Portions of the riparian zone adjacent to agricultural land were most heavily affected by alien plants, with alien species accounting for 81% of relative vegetation cover in these areas and native species accounting for only 19% (Fig. 2). Portions of the riparian zone bordered by urban and communal grazing areas showed an intermediate level of invasion, with alien species accounting for 66% of relative vegetation cover, while native species maintained a cover of 34% adjacent to these areas. Invasion

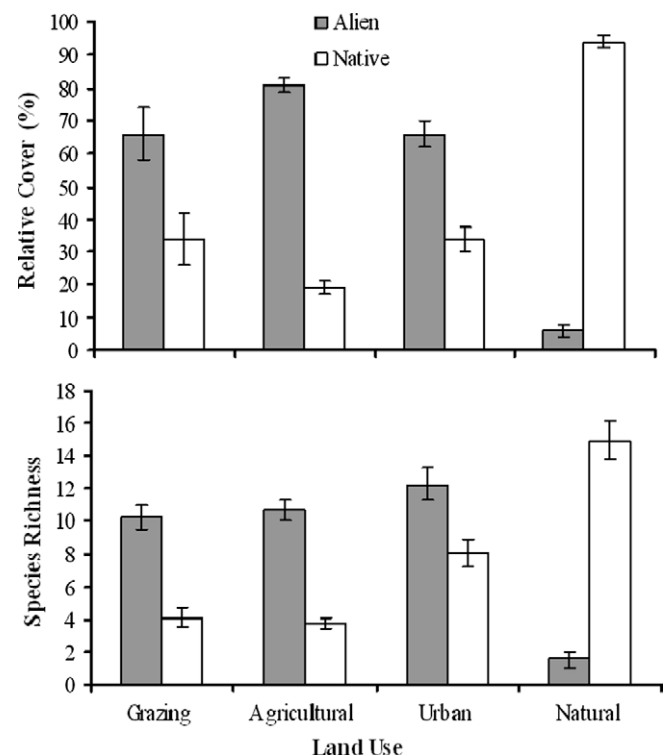


Fig. 2. Relative cover and richness of alien and native plant species along the Eerste River in relation to adjacent land-use. Bars show the standard error.

by alien species was low in areas of the river bordered by natural land, with alien species accounting for only 6% of relative vegetation cover while native species maintained a cover of 94% in these areas. Variance in alien cover was greatest among sites in communal grazing areas, where some sites are dominated almost entirely by herbaceous alien species, while other sites have dense native cover of fast growing sedges, reeds, and willow species. Representative photos of the vegetation in each land-use category can be found in [Appendix B](#).

Species richness of alien plants, as well as combined richness of alien and native species, was highest in the urban areas in and around Stellenbosch ([Fig. 2](#)). Despite the increased opportunity for propagule introduction, richness of alien species showed a decreasing trend as the river flows downstream through agricultural and communal grazing lands towards the estuary. Both species richness and cover of alien plants were low in portions of the riparian zone flanked by natural areas.

3.1. Differences in vegetation structure among plots

Measures of cover, richness, and diversity all differed significantly among land-use types according to Kruskal–Wallis ANOVA ($P < 0.01$ in all cases; [Table 3](#)). The analysis was rerun excluding plots adjacent to natural areas in order to determine whether significance values were being caused solely by differences in natural

and transformed areas. Results of the analysis which included only transformed land uses proved to be very similar to the first run. While chi-squared values dropped precipitously in some cases, differences among all of the species measures remained significant ($P < 0.01$), with the exception of alien richness ($P = 0.48$). These results suggest a strong connection between vegetation community structure and land-use in the surrounding landscape.

3.2. Differences in vegetation structure between land-use types

Results of Mann–Whitney U tests showed plots adjacent to grazing and agricultural areas to differ significantly only in cover of alien species ($P < 0.01$), while differences between agricultural and urban plots were significant for all measures except alien richness ([Table 4](#)). Native species richness was significantly different for plots adjacent to urban and grazing areas ($P < 0.01$), but native cover was not. These patterns can be explained by both the high level of alien transformation seen adjacent to agricultural lands, as well as the remnant patches of native vegetation found throughout urban and grazing areas along the river. Both grazing and agricultural plots differed significantly from plots adjacent to natural areas in all measures except total species richness. Urban plots, on the other hand, differed significantly from natural plots in respect to cover and richness of alien/native species, but not for indices of diversity. Diversity indices appeared to be effected most

Table 3

Results of Kruskal–Wallis ANOVA comparing plots adjacent to differing land-use types in relation to measures of plant species cover, richness and diversity. As multiple comparisons were involved, α values were adjusted using Bonferroni correction. (a) Shows results of the analysis of all land-use types (communal grazing, agriculture, urban, and natural; $N = 150$; significant at $P \leq .008$); (b) gives results of the analysis of transformed land uses only (communal grazing, agriculture, and urban; $N = 117$; significant at $P \leq .016$).

	(a) All land-use types				(b) Transformed land-use only			
	Df _{groups}	Df _{error}	χ^2	P	Df _{groups}	Df _{error}	χ^2	P
Cover aliens	3	146	79.4	<0.001	2	114	9.8	0.007
Richness aliens	3	146	65.3	<0.001	2	114	1.5	0.481
Cover natives	3	146	78.8	<0.001	2	114	17.2	<0.001
Richness natives	3	146	67.8	<0.001	2	114	21.6	<0.001
Total richness	3	146	13.5	0.004	2	114	12.8	0.002
Shannon–Weiner index	3	146	22.4	<0.001	2	114	18.6	<0.001
Simpson's index	3	146	21.2	<0.001	2	114	17.1	<0.001
Pielou's evenness	3	146	19.6	<0.001	2	114	11.6	0.003

Table 4

Results of Mann–Whitney U tests comparing differences among plots in relation to measures of species cover, richness and diversity. Differences between adjacent transformed land uses are shown in (a), while differences between adjacent transformed land uses and adjacent natural areas are shown in (b). As multiple comparisons were involved, α values were adjusted using the sequential Bonferroni procedure ([Rice, 1989](#)). Significant differences are indicated by asterisks.

	Grazing/agriculture N = 82				Agriculture/urban N = 101				Urban/Grazing N = 68			
	Df _{error}	U	Z	P	Df _{error}	U	Z	P	Df _{error}	U	Z	P
(a)												
Cover aliens	80	302	−2.7	0.008*	99	836	−2.3	0.023*	49	235	−0.9	0.356
Richness aliens	80	507	−0.3	0.801	99	977	−1.3	0.203	49	265	−0.3	0.752
Cover natives	80	437	−1.1	0.284	99	562	−4.2	<0.001*	49	207	−1.5	0.138
Richness natives	80	477	−0.6	0.545	99	524	−4.5	<0.001*	49	141	−2.8	0.005*
Total richness	80	482	−0.5	0.590	99	680	−3.4	0.001*	49	158	−2.5	0.013
Simpson's index	80	512	−0.2	0.847	99	612	−3.9	<0.001*	49	131	−3.0	0.002*
Pielou's evenness	80	447	−1.0	0.340	99	725	−3.1	0.002*	49	155	−2.5	0.011*
	N = 49				N = 99				N = 68			
(b)												
Cover aliens	47	20	−5.3	<0.001*	97	9	−8.0	<0.001*	66	22	−6.9	<0.001*
Richness aliens	47	14	−5.5	<0.001*	97	114	−7.3	<0.001*	66	41	−6.7	<0.001*
Cover Natives	47	31	−5.0	<0.001*	97	24	−7.9	<0.001*	66	70	−6.2	<0.001*
Richness Natives	47	32	−5.0	<0.001*	97	119	−7.2	<0.001*	66	215	−4.5	<0.001*
Total Richness	47	222	−0.9	0.363	97	926	−1.2	0.226	66	392	−2.3	0.023
Simpson's Index	47	147	−2.5	0.013*	97	682	−3.0	0.002*	66	535	−0.5	0.598
Pielou's Evenness	47	147	−2.5	0.013*	97	634	−3.4	0.001*	66	422	−1.9	0.056

heavily by altitudinal gradients, with plots in high elevation (>100 m) urban and natural areas differing significantly from plots in low elevation (<100 m) agricultural and grazing areas. Diversity indices did not, however, differ significantly between land uses within these two altitudinal zones.

3.3. Distribution analysis for common alien species

While there were many alien species which were present across several land-use types, the distributional analysis of some common alien plants revealed distinct patterns of land-use preference among certain species (Fig. 3). Species such as *Euphorbia helioscopia* and *Hordeum murinum* are prevalent in highly disturbed communal grazing areas, but were not widespread adjacent to any other land-use types. Several alien species, including *Acacia mearnsii*, *Quercus robur*, and *Tropaeolum majus*, were very common in both agricultural and urban areas, but their ranges did not extend into natural or communal grazing areas. Alien plants that were found only adjacent to urban areas include such ornamental species as *Cinnamomum camphora*, *Ligustrum ovalifolium*, and *Quercus palustris*. Very few alien species, with the exception of *Pittosporum undulatum*, have effectively invaded riparian areas adjacent to natural land.

3.4. Land-use and plant community composition

Results of the CCA suggest that patterns of plant species composition are directly related to land-use (Fig. 4). The eigenvalue ($\lambda = .764$) for the first canonical axis was highly significant ($P = 0.001$) according to the Monte Carlo permutation test, imply-

ing that the species data are well explained by the chosen land-use variables. The species–environment correlation, measuring the strength of the relationship between species and land-use, was 0.963. Monte Carlo tests for all canonical axes combined further suggested that the relationship between species composition and environmental variables was highly significant ($P = 0.001$). Axis 1 was positively correlated with natural area and negatively correlated with urban/agricultural/grazing area. As such, axis 1 can be interpreted as a gradient of land transformation. There was a clear distinction between land-use types, with the greatest divide existing between natural and other land-use variables. Another clear divide in composition existed between species adjacent to urban/agricultural lands and species adjacent to communal grazing lands. The roughly orthogonal position of natural, agricultural, and grazing variables suggests that they each control separate aspects of species composition. Urban land-use variables did not explain species composition as well as the other environmental variables. This is likely due to the fact that urban areas share many common species with adjacent agricultural and natural lands. Alien species were absent adjacent to the natural area variable, but became dominant among the other landscape variables. A few native species did stand out amidst the transformed land-use variables including *Kiggelaria africana*, *Olea europaea* subsp. *africana*, and *Salix mucronata* subsp. *mucronata*, among others.

Land-use variables were strongly supported by corresponding soil variables, further explaining patterns of plant species composition along the Eerste River. Soil electrical resistance was highly correlated with natural area, suggesting that pure sand soils can be found mostly amongst natural vegetation. Concentrations of carbon were highly correlated with adjacent urban lands, while high

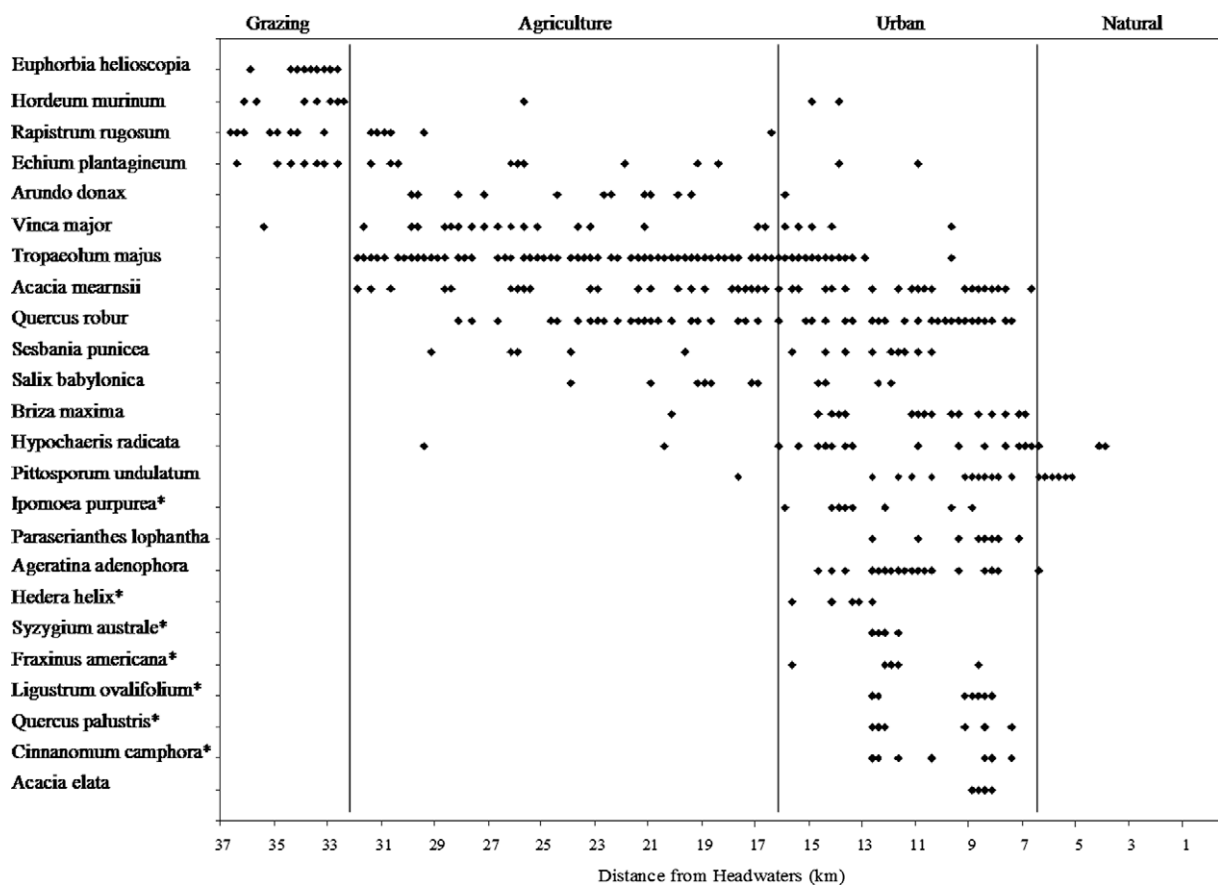


Fig. 3. Distribution of some common alien plant species along a gradient of land-use types adjacent to the Eerste River, Western Cape, South Africa. Divisions in predominant land-use along the length of the river are shown across the top. Species marked with (*) are primarily ornamental and garden species. Occurrence of species is represented by (♦).

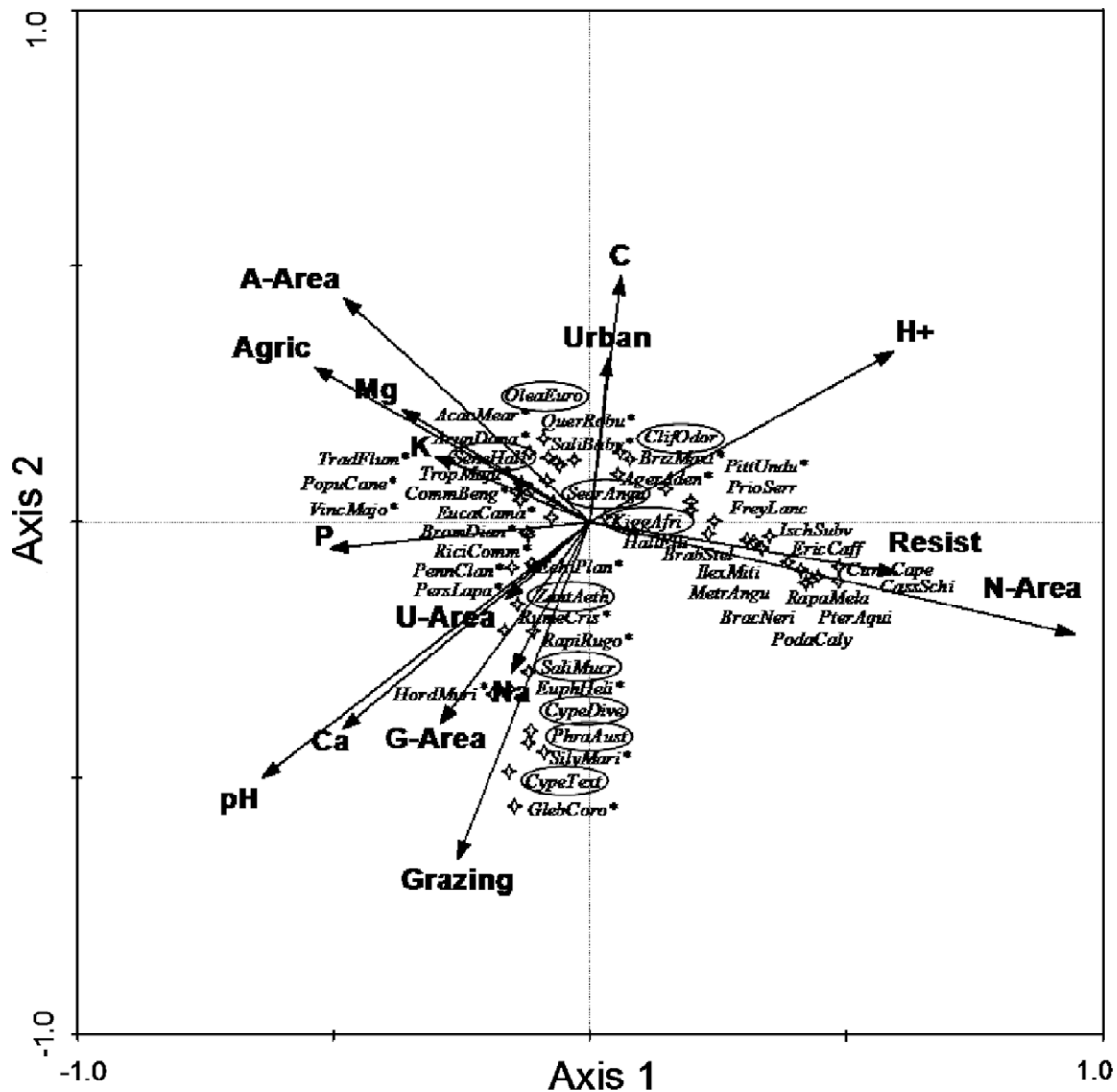


Fig. 4. Canonical correspondence analysis (CCA) ordination diagram showing species scores as a function of the first two axes, with respect to environmental and soil variables. Importance of each environmental variable and its influence on species composition is indicated by the length of its arrow. For legibility reasons, only species having the greatest weight are shown. Species abbreviations are based upon the first four letters of the generic and specific names. Alien species are indicated by (*). Circled species are those native species which continue to persist within transformed land-use types. Full species names can be found in [Appendix A](#). For explanation of environmental variables see [Table 1](#).

concentration of the soil nutrients magnesium, potassium, and phosphorous were correlated with agricultural land-use variables. Sodium, calcium, and pH were all highly correlated with grazing lands in the lower reaches of the river.

4. Discussion

Results of this study suggest that species composition along riparian zones is strongly affected by land-use and corresponding soil properties in the surrounding landscape. These findings accord with results from similar studies which show a distinct species gradient between urban and rural land-use types (McDonnell *et al.*, 1997; Moffatt *et al.*, 2004; Burton *et al.*, 2005). The results of the current study differ in that they show riparian zones in agricultural areas to be more highly altered by alien plant invasion than those in urban areas.

Very few native species have managed to survive in areas of the riparian zone adjacent to agricultural land. This may be the result

of increased nutrient inputs from agricultural fields giving alien species a competitive advantage over natives. Growth of the aggressive alien invader *Arundo donax*, a species common along agricultural areas of the Eerste River (Fig. 3) and rivers throughout the southern US, has been found to be positively affected by nitrogen enrichment of soils (Quinn et al., 2007). Conversely, very few aliens have expanded into areas of the river adjacent to natural land. The buffer of natural vegetation between the river and forestry plantation has been very effective at excluding the highly invasive *P. radiata* from the riparian zone, suggesting that maintenance of buffer zones of natural vegetation should be a key strategy for conservation where these buffers still exist. An additional barrier to expansion of alien populations appears to be provided by the Kleinplaas Dam, above which nearly all plots were devoid of alien species. As described earlier, areas upstream of the dam are the only portions of the river which maintain their natural flow regime. Altered hydrology, and therefore changes in natural disturbance patterns, may thus be playing a key role in establishment of alien species downstream of the dam. This has been shown to be

the case in both Arizona and Montana where river regulation has led to the expansion of populations of the alien invaders *Elaeagnus angustifolia* and *Tamarix ramosissima* respectively (Lesica and Miles, 1999; Shafroth et al., 2002).

In contrast to results presented by Burton and Samuelson (2008), vegetation plots in urban areas were found to be significantly richer in species than plots adjacent to other land uses. This is likely the combined result of remnant native vegetation clusters and urban/suburban gardens acting as important propagule sources for introduction of native and alien taxa. This has been shown to be an important factor structuring alien plant floras throughout South Africa and other areas of the world (Reichard and White, 2001; Alston and Richardson, 2006; van Kleunen et al., 2007; Foxcroft et al., 2008). Distributional analysis of species showed a total of 27 alien species which were exclusive to plots in urban areas, including almost all of the ornamental alien species. While the density of many of these species suggests that they are highly effective invaders of urban riparian zones, they have not yet expanded beyond the boundaries of these developed areas. Reasons for this pattern are unclear. Many of the species unique to these plots may be fairly recent introductions as fashionable plants for gardens and hedges (e.g. *Ligustrum ovalifolium*, *Syzygium australe*). Increasing propagule pressure and the spread of established populations may well allow for expansion of these populations into other land-use types over time. This has been the case in both the United States (for woody species) and Australia (for woody and herbaceous species), where a majority of naturalized alien species were originally introduced intentionally for horticultural purposes (Reichard and White, 2001).

Results of the CCA allowed for the identification of native riparian plants that are able to persist in areas of high alien invasion. Robust natives, such as the willow *Salix mucronata* subsp. *mucronata*, are able to thrive even in communal grazing areas with intermediate levels of disturbance. While this willow is highly palatable to grazing animals, it appears capable of rapid growth once grazers are removed. One riparian vegetation plot dominated by herbs when visited in October had become a dense willow thicket when revisited in December. Because of its persistence and role in stabilizing banks, this species is recommended as a key species for restoration projects in wet bank situations along rivers of the Cape Floristic Region (Holmes et al., 2008). Other robust native species such as *Kiggelaria africana* and *Olea europaea* subsp. *africana*, while not particularly fast growers, appear tolerant of shady conditions and competition from alien species, even in highly transformed agricultural areas. These species play an important ecological role as they produce foliage and fruits that are highly sought after by native bird and invertebrate species (Richardson and Fraser, 1995; Venter and Venter, 1996). Due to an aggressive root system, *O. europaea* subsp. *africana* can also be very effective at stabilizing river banks and preventing soil erosion (Venter and Venter, 1996). Most studies which have provided suggestions for restoration of riparian vegetation in the Cape Floristic Region have centered on the pristine native assemblages found in headwaters systems rather than on highly invaded areas in the lower reaches (Prins et al., 2004; Sieben and Reinecke, 2008). Due to extensive land transformation along the lower reaches of the Western Cape's river systems, very little is known about which native species would be expected in these areas without human influence. As such, the persistent native species identified in the CCA will be valuable focal species for any future restoration attempts.

Given the level of change these ecosystems have undergone, restoration of highly invaded riparian areas to a species composition resembling that of natural areas is probably not feasible. Rather, these assemblages should be considered good examples of novel ecosystems, i.e. ecosystems which have emerged or are emerging as the result of anthropogenic actions and which now

comprise taxa that have limited shared evolutionary history (Hobbs et al., 2006). In the coming decades, human activity in riparian zones is likely to increase in both magnitude and complexity. It is important to consider the most appropriate management responses in these areas. We suggest that management should focus on ecosystem functioning and resilience rather than native species purity (Seastedt et al., 2008). In some cases, these novel ecosystems may already be functioning as effectively as the ecosystems that were present prior to human intervention. Alien plants may even be securing services that were not historically provided by native species, but which have now become important (i.e., appreciated by humans) within the novel ecosystem. For example, dense herbaceous mats along the riparian zone, such as those created by *Commelina benghalensis* and *Tradescantia fluminensis*, are probably effective at preventing excess soil and nutrients from entering water courses. These services were historically unnecessary but have become important under the current land-use regime. Consequently, removal of these species could be detrimental from both ecological and social perspectives. Not all novel ecosystems will maintain or provide new ecosystem services and, hence, not all should be accepted. Dense thickets of *Arundo donax* occur in riparian ecosystems in many parts of the world. Monospecific stands of this species may provide some ecosystem services, but the negative influences of dense stands (by increasing the amount and especially the vertical continuity of fuel, causing more intense fires and carrying fires into the crown; Brooks et al., 2004) usually outweigh any potentially positive influence. In such cases, management resources would be well used in removing the transformer species and restoring desired ecosystem functions. In other cases, novel ecosystems may present trade-offs that need to be carefully weighed against each other. An example is the invasive Australian tree *A. mearnsii*; dense stands of this phreatophytic species reduce streamflow in many parts of South Africa (Dye and Jarman, 2004). Nonetheless, some landowners and residents are loathe to sanction clearing stands of this species because of its aesthetic appeal and use by some wildlife species. Its existence in urban/agricultural areas is thus seen as enhancing the quality of life for many residents, human and animal; this must be weighed against the negative consequences of increased transpiration.

Not all ecosystem services can be attained at every site and so managers and planners need to decide what type of intervention, if any, is appropriate to provide the desired functions. In areas where restoration is warranted, the first priority should be to install nodes of key riparian species that will hasten the return of desired ecosystem services (Holmes et al., 2005, 2008). In the case of highly human-modified landscapes such as the lower reaches of the Eerste River catchment, it seems wise not to allocate substantial resources in attempting to remove species which may be part of a new, and functional, ecosystem. In less developed localities, such as in large protected areas, systematic clearing of alien species may well be warranted (and feasible) to maintain the integrity and natural functioning of ecosystems.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.09.021.

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